Nonequilibrium coexistence in a competition model with nutrient storage

Revilla Rimbach, T.A.; Weissing, F.J.

Published in:
Ecology

DOI:
10.1890/07-1103.1

Ecology, 89(3), 2008, pp. 865–877

NONEQUILIBRIUM COEXISTENCE IN A COMPETITION MODEL WITH NUTRIENT STORAGE

Tomás Revilla and Franz J. Weissing[1]

Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

Abstract. Resource competition theory predicts that, in equilibrium, the number of coexisting species cannot exceed the number of limiting resources. In some competition models, however, competitive interactions may result in nonequilibrium dynamics, allowing the coexistence of many species on few resources. The relevance of these findings is still unclear, since some assumptions of the underlying models are unrealistic. Most importantly, these models assume that individual growth directly reflects the availability of external resources, whereas real organisms can store resources, thereby decoupling their growth from external fluctuations. Here we study the effects of resource storage by extending the well-known Droop model to the context of multiple species and multiple resources. We demonstrate that the extended Droop model shows virtually the same complex dynamics as models without storage. Depending on the model parameters, one may obtain competitive exclusion, stable equilibrium coexistence, periodic and non-periodic oscillations, and chaos. Again, nonequilibrium dynamics allows for the coexistence of many species on few resources. We discuss our findings in the light of earlier work on resource competition, highlighting the role of luxury consumption, trade-offs in competitive abilities, and ecological stoichiometry.

Key words: *Droop model; ecological stoichiometry; luxury consumption; Monod model; oscillations and chaos; Redfield ratios; resource competition; resource uptake; supersaturation; trade-offs.*

Introduction

Many resource competition models have the property that, in a homogeneous environment and at equilibrium, the number of coexisting species is limited by the number of limiting resources (Grover 1997). As noticed already by Hutchinson (1961), this creates the paradox of how to explain the coexistence of many species on a small number of resources. Traditional attempts to resolve the paradox tend to invoke spatial heterogeneity or externally imposed fluctuations (e.g., seasonal variation in nutrient supply or oscillations induced by predator–prey or host–parasite interactions) in order to create the nonequilibrium conditions required to maintain high levels of biodiversity (Hutchinson 1961, Armstrong and McGehee 1980).

More recently, Huisman and Weissing (1999, 2001, 2002) demonstrated that, even in a homogeneous and constant environment, multispecies competition does not necessarily lead to equilibrium. In fact, the competition process itself may generate oscillations and chaos. Such nonequilibrium conditions allow "supersaturation" (Schippers et al. 2001), i.e., the coexistence of many more species than there are limiting resources. It crucially depends on the relationship between resource requirements and resource consumption patterns whether competition leads to equilibrium or to ongoing fluctuations (Huisman and Weissing 2001, Huisman et al. 2001). If species tend to consume most of the resources for which they have low resource requirements, competitive exclusion will result where the initial conditions decide upon who will win the competition. If species tend to consume most of those resources for which they have high resource requirements, then equilibrium coexistence is to be expected, where the number of species does not exceed the number of resources. Finally, oscillations and supersaturation are to be expected if species tend to consume most of those resources for which they have intermediate requirements. These results are supported by mathematical analysis (Huisman and Weissing 2001, Li 2001, Li and Smith 2003) and numerical simulations (Huisman et al. 2001).

The conclusions of Huisman and Weissing were based on the Monod model, which is one of the standard models of resource competition theory (León and Tumpson 1975, Tilman 1982, Grover 1997). However, this model employs some unrealistic assumptions, making it difficult to judge the empirical relevance of the above predictions. Most importantly, the model assumes that individual growth reflects the external availability of resources, whereas many organisms are able to store resources and hence are more dependent on their individual internal resource content, called quota. Much recent work on multiple nutrient limitation (Legovic and Cruzado 1997, Klausmeier et al. 2004*b*), dynamic energy budgets (Kooijman 2000), and ecological stoichiometry in phytoplankton (Klausmeier et al.

Manuscript received 6 July 2007; accepted 19 July 2007. Corresponding Editor: A. M. de Roos.

[1] Corresponding author. E-mail: f.j.weissing@rug.nl

2004*a*) shows the importance of a more mechanistic description of resource uptake, internal resource storage, and quota-dependent growth. The so-called quota models describe the dynamics of resource acquisition and population growth separately and they often provide a better description of competition than models without storage, in particular in fluctuating environments (Grover 1997, Ducobu et al. 1998). On the other hand, quota models contain many more parameters and dynamic variables, making their analysis much more difficult. It is therefore not surprising that quota models have never been as popular as Lotka-Volterra models or Monod-type of models for resource competition.

Still, it is important to investigate whether the conclusions of classical resource competition theory are robust with respect to plausible extensions of the underlying models, e.g., by taking storage and quota-dependent growth into account. In particular, it is by no means self-evident that the results of Huisman and Weissing still apply in the presence of nutrient storage. One might argue that storage will diminish the effects of external resource shortage and therefore help to protect numerically abundant species against invaders. Since repeated invasions are crucial for competition-induced oscillations and supersaturation, one might conjecture that nonequilibrium conditions are of minor importance in quota models. On the other hand, quota models have more degrees of freedom, they contain more nonlinearities, and they incorporate implicit time delays caused by the separation of uptake and growth. Since all these factors favor nonequilibrium conditions, one might conjecture that just quota models have a higher potential for oscillations and supersaturation. To settle this issue, we here study the Droop model (Droop 1973, Tilman 1977, Grover 1997, Legovic and Cruzado 1997), which is currently viewed as the standard quota model of resource competition. By means of a simulation approach, we ask the question whether and to what extent the conclusions of (Huisman and Weissing 2001) are affected by nutrient storage. Is it, for example, more or less likely that oscillations and supersaturation do occur in the presence of nutrient storage?

Models and Definitions

The multispecies Monod model

Huisman and Weissing (1999, 2001) studied the multispecies extension of a classical resource competition model (Leon and Tumpson 1975, Tilman 1982) where the densities N_i (individuals per volume) of n species and the concentrations R_j (mass per volume) of k resources are governed by a system of ordinary differential equations:

$$\frac{dN_i}{dt} = N_i[\mu_i(R_1, \ldots, R_k) - m_i] \tag{1a}$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} c_{ji}\mu_i(R_1, \ldots, R_k)N_i \tag{1b}$$

where D is the resource flow rate, S_j is the input concentration of resource j, and c_{ji} is the fixed content of resource j in species i (mass per individual). In this system, the specific growth rate of species i ($[1/N_i]dN_i/dt$) is given by the difference between the specific growth rate μ_i and the specific mortality rate m_i. Mortality rates are assumed to be constant, while the growth rates are functions of the (external) levels of resources $R_1, \ldots, R_k$. Usually, μ_i is assumed to be given by a combination of Monod's (1950) equation and Liebig's (1840) law of the minimum:

$$\mu_i(R_1, \ldots, R_k) = r_i \min_j\left(\frac{R_j}{H_{ji} + R_j}\right) \tag{2}$$

where r_i is the maximal specific growth rate of species i under resource saturation, and H_{ji} is the half-saturation constant of resource j for species i. For brevity, we will call the system defined by Eqs. 1 and 2 the Monod model. The properties of this system are well known (e.g., Tilman 1982, Huisman and Weissing 2001). To a large extent, they depend on the resource supply point $\mathbf{S} = (S_1, \ldots, S_k)$, the consumption vectors $\mathbf{c}_i = (c_{1i}, \ldots, c_{ki})$, and the minimal resource requirements $\mathbf{R}_i^* = (R_{1i}^*, \ldots, R_{ki}^*)$ of the various species. Here, the resource requirement R_{ji}^* of species i with respect to resource j is that concentration of resource j for which mortality is just balanced by growth ($m_i = \mu_i$), given that all other resources are present in excess. In brief, Huisman and Weissing (2001) arrived at the following conclusions:

1) At equilibrium, each species is limited by a different resource. Accordingly, no more species can coexist than there are limiting resources.

2) If each species tends to consume most of that resource for which it has the lowest requirement (i.e., the lowest R_{ji}^*), species-poor equilibrium systems are to be expected where a single competitor excludes all others.

3) If each species tends to consume least of that resource for which it has the lowest requirement, then saturated equilibrium systems are to be expected, where the number of coexisting species corresponds to the number of limiting resources.

4) If species tend to consume most of the resources for which they have intermediate requirements, then oscillations and chaos allowing supersaturation (i.e., the coexistence of more species than limiting resources) are to be expected.

The multispecies Droop model

In the Monod model, all species are assumed to have fixed resource contents (c_{ji}) and species growth is directly dependent on the external resource concentrations. In case of microorganisms (e.g., phytoplankton), for which the Monod model was designed, it is more plausible to assume that the internal resource content can fluctuate (e.g., due to storage) and that growth more reflects internal resource concentrations than external resource availabilities. To model this, we use an

extension of the variable stores model of Droop (1973) to n consumers and k resources. This model considers a third set of variables in addition to the species and resources: the internal resource content or quota Q_{ji} of resource j for species i. The quota is the variable equivalent of the fixed resource content c_{ij} in the Monod model, both having units of mass of resource per individual. The dynamical equations are

$$\frac{dN_i}{dt} = N_i[\mu_i(Q_{1i}, \ldots, Q_{ki}) - m_i] \tag{3a}$$

$$\frac{dQ_{ji}}{dt} = f_{ji}(R_j) - \mu_i(Q_{1i}, \ldots, Q_{ki})Q_{ji} \tag{3b}$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} f_{ij}(R_j)N_i. \tag{3c}$$

Notice that the equations for population growth (Eq. 3a) correspond to Eq. 1a of the Monod model, with the sole difference that the growth functions μ_i do not depend on external resource concentrations but on internal quotas. The resource equations (3c) correspond to Eq. 1b of the Monod model, but now the specific resource uptake is described by functions $f_{ji}(R_j)$ rather than fixed consumption vectors. Eq. 3b characterizes the quota dynamics, which is governed by the resource uptake per individual [i.e., $f_{ji}(R_j)$] and dilution of quota due to growth and/or reproduction [accounted for by the term $\mu_i(Q_{ji})$].

Following Tilman (1977) and Legovic and Cruzado (1997), we assume that the growth rate μ_i is governed by a combination of Liebig's law of the minimum and Droop's (1973) formula relating growth and quotas:

$$\mu_i(Q_{1i}, \ldots, Q_{ki}) = r_i \min_j \left(1 - \frac{q_{ji}}{Q_{ji}}\right) \tag{4}$$

where r_i is the maximum growth rate under quota saturation and q_{ji} is the minimum subsistence quota for resource j: for $Q_{ji} > q_{ji}$ the growth rate is positive, but it is set to zero if $Q_{ji} < q_{ji}$. According to Eq. 4, at any given moment the growth of species i depends only on the nutrient having the smallest internal content relative to the subsistence quota.

Uptake of resources from the external medium is assumed to be an increasing and saturating function of the external resource concentration:

$$f_{ji}(R_j) = \frac{v_{ji}R_j}{K_{ji} + R_j} \tag{5}$$

where v_{ji} and K_{ji} are the maximum uptake rate and the uptake half-saturation constant for resource j by species i, respectively.

For brevity, we will call the system defined by Eqs. 3, 4, and 5 the Droop model for the rest of the paper.

At first sight, the Monod and the Droop model seem to share many properties. It is, however, important to be aware of some crucial differences:

1) Although the dependence of μ_i on R_j for the Monod model (Eq. 2) and f_{ji} on R_j for the Droop model (Eq. 5) are topologically identical functions, they describe different (though related) processes. In fact, f_{ji} can be given the same kind of mechanistic underpinning (based on handling time arguments) as a "functional response" of Holling type II (Aksnes and Egge 1991). In contrast, the Monod terms in Eq. 2 correspond to a "numerical response" of consumer density toward changes in resource availability. Since metabolism is much more complex than resource uptake, there is at present no general and simple theory providing a mechanistic underpinning for the numerical response. Accordingly, the Monod-type numerical response (Eq. 2) in the Monod model and the Droop-type numerical response (Eq. 4) in the Droop model both represent empirical relationships that are not yet linked to underlying mechanisms.

2) Although there is an obvious correspondence between some of the variables and parameters of the two models, the relationship between the models is less straightforward than one might think. For example, the parameter r_i corresponds to maximum growth rates in both models. Still there is an important difference. In the Monod model, r_i corresponds to the growth rate of species i achieved asymptotically when all resources are overabundant. In the Droop model, this is not the case. Here an infinite availability of all resources saturates the uptake but not the growth rate. Even if uptake rates are maximal, the quotas do not exceed some limit values, leading to growth rates μ_i that can be substantially smaller than r_i.

3) For the reason indicated above, the simpler Monod model is not just a special case of the more complex Droop model. Burmaster (1979) derived a mapping between both models, but it only holds for the characterization of the community equilibrium in case of a single consumer growing on a single resource. In case of more than one resource, the relationship between the models is rather intricate, even if the quota dynamics is rather fast and quotas are at a quasi-steady state all the time.

Resource requirements and consumption patterns

As indicated above, the dynamics of the Monod model is governed to a large extent by the relation between resource requirements and resource consumption patterns. We therefore start by defining the same concepts for the Droop model. In contrast to the Monod model, we now have to distinguish between external and internal resource requirements, while the consumption pattern of a species is no longer characterized by a fixed consumption vector.

The internal requirement Q_{ji}^* of species i for resource j is defined as the quota Q_{ji} for which mortality is just balanced by growth ($m_i = \mu_i$), given that the quota of all other resources are not limiting growth. In view of Eqs. 3a and 4 Q_{ji}^* is given by the following:

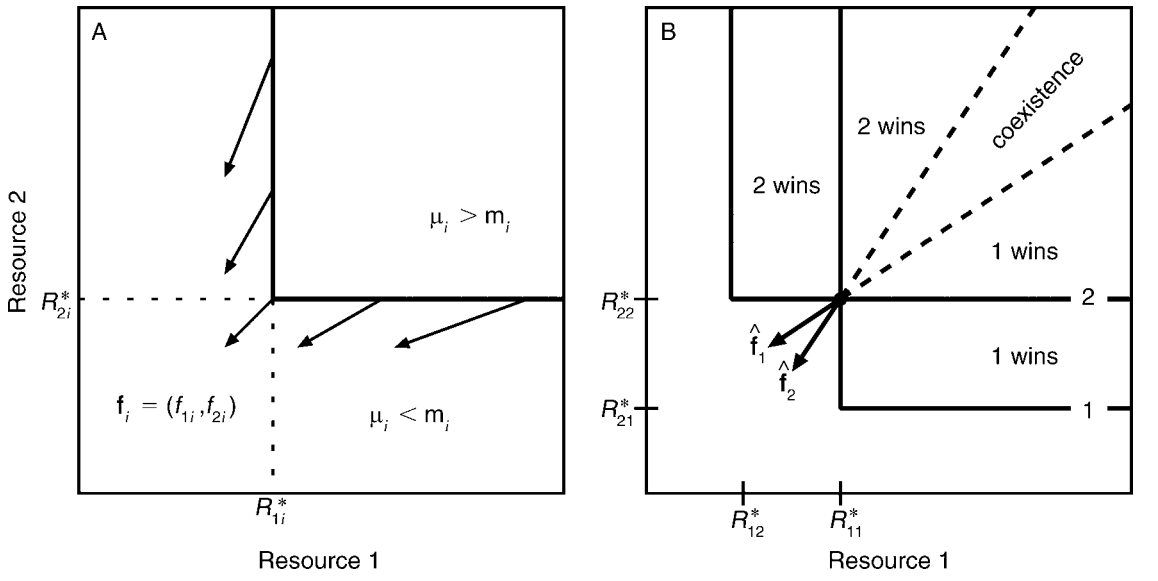

FIG. 1. Two-dimensional resource space illustrating competition for two limiting resources. (A) For each species i, an L-shaped nullcline divides the resource space into an area where net growth occurs ($\mu_i > m_i$) and an area where species i does decline ($\mu_i < m_i$). The nullcline is determined by the minimal resource requirements R^*_{1i} and R^*_{2i}. The consumption vector $\mathbf{f}_i = \mathbf{f}_i(R_1, R_2)$ of species i depends on the resource concentrations. The slope of $\mathbf{f}_i$ increases along the vertical segment of the nullcline and decreases along the horizontal segment. (B) A two-species community equilibrium exists if the two nullclines cross and the supply point falls inside the wedge defined by the consumption vectors $\hat{\mathbf{f}}_1$ and $\hat{\mathbf{f}}_2$ of the two species (designated 1 and 2) at the intersection point. If each species consumes most of the resource limiting its own growth (the configuration shown here), the community equilibrium is stable.

$$Q^*_{ji} = r_i q_{ji}/(r_i - m_i). \tag{6}$$

We can now define the external requirement R^*_{ji} of species i for resource j as that resource concentration R_j just allowing to achieve the quota Q^*_{ji}, given that the quota of all other resources are not limiting growth. R^*_{ji} is obtained by setting Eq. 3b equal to zero, given that $\mu_i = m_i$ and $Q_{ji} = Q^*_{ji}$. This implies $f_{ji}(R^*_{ji}) = m_i Q^*_{ji}$ or equivalently

$$R^*_{ji} = \frac{K_{ji} m_i Q^*_{ji}}{v_{ji} - m_i Q^*_{ji}}. \tag{7}$$

As in the Monod model, the parameter R^*_{ji} summarizes the competitive ability of species i for a given resource j. Whenever the resource concentration R_j is below R^*_{ji}, species i will decline. Hence, if competition occurs for a single resource only, the species with the lowest requirement will exclude all the others (Smith and Waltman 1994), which is known as the R^*-rule (Grover 1997).

In resource space, the set of external resource requirements R^*_{ji} define the nullcline (or zero net growth isocline) of species i: $R_j > R^*_{ji}$ implies that $\mu_i > m_i$ and species i can grow; while i decreases for $R_j < R^*_{ji}$. In case of two resources, the resource space (R_1, R_2) is two dimensional, and the nullclines are L-shaped, indicative of a sharp switch in the identity of the limiting resource (Fig. 1A). This concept can be extended to higher dimensional resource spaces ($R_1, \ldots, R_k$) where the planes $R_j = R^*_{ji}$ define the nullclines.

The consumption vector (or consumption pattern) of species i is given by i's specific consumption rates $f_{ji}(R_j)$ of the different resources. In the Monod model, the consumption vector of species i is given by $\mathbf{c}_i = (c_{1i}, \ldots, c_{ki})$ and hence independent of the resource availabilities. In the Droop model, however, the direction of the consumption vector $\mathbf{f}_i(\mathbf{R}) = [f_{1i}(R_1), \ldots, f_{ki}(R_k)]$ strongly reflects the external resource concentrations. Fig. 1A illustrates this change in the direction of the consumption vectors in a two-dimensional resource space. If we keep resource 1 fixed at its requirement ($R_1 = R^*_{1i}$) and if we increase the level of resource 2 above its requirement ($R_2 > R^*_{2i}$), then the component of the consumption vector corresponding to resource 2 increases with respect to the one of resource 1. The same applies mutatis mutandis for changes in resource 1. This behavior is associated with the accumulation of higher levels of non-limiting resources at equilibrium, a phenomenon known as luxury consumption (Grover 1997).

Community equilibrium

A Droop system is at equilibrium if all rate equations (Eqs. 3a–c) are equal to zero: $dN_i/dt = dQ_{ji}/dt = dR_j/dt = 0$. Dynamic variables at equilibrium will be indicated by a hat (^). An equilibrium will be called a community equilibrium if $n \geq 2$, $k \geq 2$, and all dynamical variables are positive $\hat{N}_i > 0$, $\hat{Q}_{ji} > 0$, $\hat{R}_j > 0$. Such a state, stable or not, exists if the following conditions are met.

First, the nullclines of all coexisting species have to intersect in a single point in resource space (see Fig. 1B). This implies that at most k species can coexist at

equilibrium, since generically more than k nullclines will not have a common intersection point in k-dimensional resource space. Let us therefore assume from now on that $n = k$. Moreover, all n nullclines can only intersect if each species is limited by a different resource (see Fig. 1B). Let us therefore assume that species 1 is limited by resource 1, species 2 by resource 2, and so on. Then the equilibrium in resource space is given by

$$\hat{\mathbf{R}} = (\hat{R}_1, \ldots, \hat{R}_n) = (R^*_{11}, \ldots R^*_{nn}). \quad (8)$$

Second, the common intersection point in resource space must be attainable. This is only possible if the resource supply point $S = (S_1, \ldots, S_n)$ is located in the positive cone that is attached at the resource equilibrium $\hat{\mathbf{R}}$ and spanned by the consumption vectors $\hat{\mathbf{f}}_i = \mathbf{f}_i(\hat{\mathbf{R}}) = [f_{1i}(R^*_{11}), \ldots, f_{ni}(R^*_{nn})]$ at this equilibrium (see Huisman and Weissing [2001] for a detailed justification). Fig. 1B visualizes this cone as a wedge in a two-dimensional resource space.

The special case of two species competing for two resources has for the Droop model been studied graphically by Turpin (1988). This is depicted in Fig. 1B, where each species consumes comparatively more of the resource for which it has the highest requirement, a situation leading to stable coexistence. If, on the other hand, each species consumes more of the resource most required by the other species (corresponding to the situation where the two consumption vectors $\hat{\mathbf{f}}_1$ and in $\hat{\mathbf{f}}_2$ Fig. 1B were interchanged), competitive exclusion will result where the winner may depend on the initial conditions. Hence for $n = k = 2$, the graphical analysis is very similar to that of the simpler Monod model. Notice, however, that the slopes of consumption vectors are fixed in the Monod model, whereas they are dependent on the position in resource space in the Droop model (as illustrated in Fig. 1A).

Notice further that the equilibrium values $\hat{R}_j$ and $\hat{Q}_{ji}$ are in general not equal to resource requirements R^*_{ji} and Q^*_{ji}. The "star values" are consumer properties that are derived under the assumption that the given resource j is limiting. In contrast, the "hat values" are system properties reflecting the state of the system at equilibrium. Star and hat values only coincide for those resources that happen to be limiting at the community equilibrium, i.e., $\hat{R}_i = R^*_{ii}$ and $\hat{Q}_{il} = Q^*_{ii}$. For the nonlimiting resources ($j \neq i$), we have instead $\hat{R}_j > R^*_{ji}$, $\hat{Q}_{ji} > Q^*_{ji}$, corresponding to luxury consumption.

Results

In a separate attempt, we show how the local stability of the community equilibrium can be characterized analytically (T. Revilla and F. J. Weissing, *unpublished manuscript*). Because of the high dimensionality of the Droop model, already a local analysis is difficult, although it turns out that, as in the Monod model, the consumption patterns at equilibrium $\mathbf{f}_i(\hat{\mathbf{R}})$ plays a crucial role. We have little hope that global and nonequilibrium dynamics of the Droop model can be characterized analytically. Therefore, we see no alternative than to rely on numerical simulations.

To get a representative picture of the dynamics, we performed tens of thousands of simulations, each covering an extensive period of time. Details about parameter choice, initializations, and the numerical integration technique are given in Appendix A. The parameters used in our figures are given in Appendix B. In the majority of simulations, we focused on chemostat-like conditions where $m_i = D$. Moreover, we usually set $r_i = r$ for all species. See *Discussion* for a justification of these assumptions.

Competition for two resources

In the Monod model, competition for two resources always results in the convergence of the system to a stable equilibrium where at most two species can stably coexist (Huisman and Weissing 2001). Oscillations never occur. To check whether the same holds true for the Droop model, we ran extensive simulations of two species competing for two resources. Without exception, we found the same three dynamical scenarios that are well-known from the Monod model:

1) Species 1 always wins when it is the better competitor for both resources (i.e., $R^*_{11} < R^*_{12}$ and $R^*_{21} < R^*_{22}$); species 2 always wins when the opposite holds true (i.e., $R^*_{12} < R^*_{11}$ and $R^*_{22} < R^*_{21}$).

2) The two species stably coexist at equilibrium if the nullclines intersect and at the intersection point each species consumes most of the resource for which it has the highest requirement (i.e., Fig. 1B).

3) Either species 1 or species 2 wins (depending on the initial condition) if the nullclines intersect and each species consumes at the intersection point most of the resource for which it has the lowest requirement (i.e., Fig. 1B, but with $\hat{\mathbf{f}}_1$ and $\hat{\mathbf{f}}_2$ interchanged).

In all simulations, the system approached a steady state, and oscillations did not occur. This conclusion does not depend on the chemostat assumption ($m_i = D$) or the equality of the r_i values.

Competition for three resources

Also, in the case of more than two resources, the dynamics of competition strongly depends on the relationship between resource requirements and consumption patterns. However, a full characterization of the system behaviour seems a forbidding task. In fact, there are $(k!)^{2k}$ qualitatively different configurations of resource requirements and consumption patterns (Huisman and Weissing 2001), giving a huge number (46 656) already for $n = k = 3$. Huisman and Weissing therefore restricted their analysis to some important special cases. In the case of three resources, they were able to derive clear-cut predictions for the following three scenarios:

1) Each species consumes most of the resource for which it has the highest requirement. Prediction: stable equilibrium coexistence.

TABLE 1. The dynamics of competition for three resources strongly depends on the relationship between resource requirements (quantified by R^*-values) and consumption patterns [quantified by the elements of the consumption vectors at equilibrium $\hat{f}_{ji} = f_{ji}(\hat{R}_j)$].

Requirements	Scenario 1	Scenario 2	Scenario 3
$R^*_{11} > R^*_{12} > R^*_{13}$	$\hat{f}_{11} > \hat{f}_{12} > \hat{f}_{13}$	$\hat{f}_{12} > \hat{f}_{13} > \hat{f}_{11}$	$\hat{f}_{13} > \hat{f}_{12} > \hat{f}_{11}$
$R^*_{22} > R^*_{23} > R^*_{21}$	$\hat{f}_{22} > \hat{f}_{23} > \hat{f}_{21}$	$\hat{f}_{23} > \hat{f}_{21} > \hat{f}_{22}$	$\hat{f}_{21} > \hat{f}_{23} > \hat{f}_{22}$
$R^*_{33} > R^*_{31} > R^*_{32}$	$\hat{f}_{33} > \hat{f}_{31} > \hat{f}_{32}$	$\hat{f}_{31} > \hat{f}_{32} > \hat{f}_{33}$	$\hat{f}_{32} > \hat{f}_{31} > \hat{f}_{33}$
Prediction	equilibrium coexistence	oscillations	exclusion

Notes: For a cyclic configuration of resource requirements (where in all cases species i has the highest requirement for resource i), the table shows three different configurations of consumption patterns and the outcome predicted on the basis of the Monod model. In the first scenario, species i consumes most of the resource for which it has the highest requirement; in the second scenario, all species consume most of the resource for which it has the intermediate requirement; and in the third scenario, each of them consumes most of the resource for which its requirement is the lowest.

2) Each species consumes most of the resource for which it has the intermediate requirement. Prediction: species oscillations.

3) Each species consumes most of the resource for which it has the lowest requirement. Prediction: competitive exclusion where the winner depends on the initial condition.

In the case of the Droop model, there are even more degrees of freedom since the consumption patterns are not fixed but variable. The three scenarios above can, however, be implemented by focusing on the consumption vectors $\hat{\mathbf{f}}_i = \mathbf{f}_i(\hat{\mathbf{R}})$ at equilibrium (see Appendix A). The three scenarios and the predictions based on the Monod model are summarized in Table 1.

Fig. 2 shows some simulations of the Droop model with outcomes fully in line with the predictions derived on the basis of the Monod model. When all species consume most of the resource for which they have the highest requirements, the three species coexist stably at equilibrium (Fig. 2A). The same result was obtained by

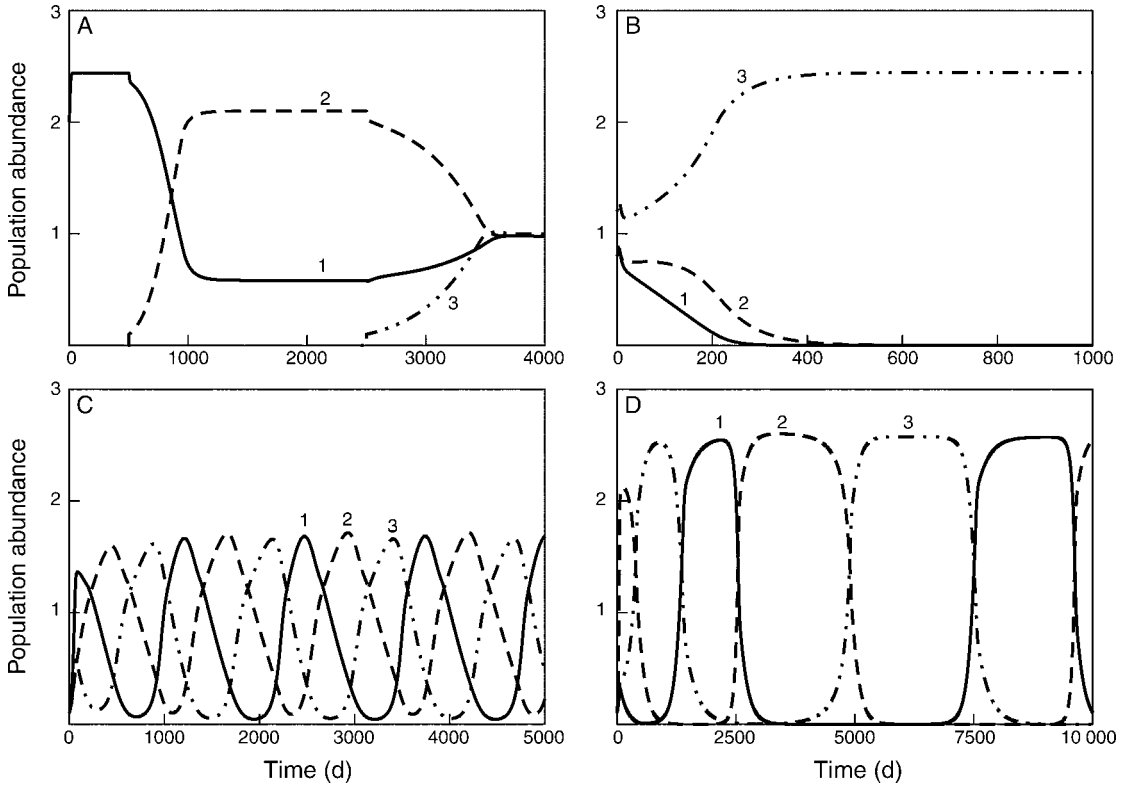

FIG. 2. Three species competing for three resources. (A) Equilibrium coexistence: species 2 invades the monoculture of species 1, the resulting two-species equilibrium is invaded by species 3, and the resulting three-species equilibrium is stable. (B) Competitive exclusion: here the initial condition favors species 3. (C) Species oscillations: convergence to a limit cycle. (D) Species oscillations of increasing period: convergence to a heteroclinic cycle.

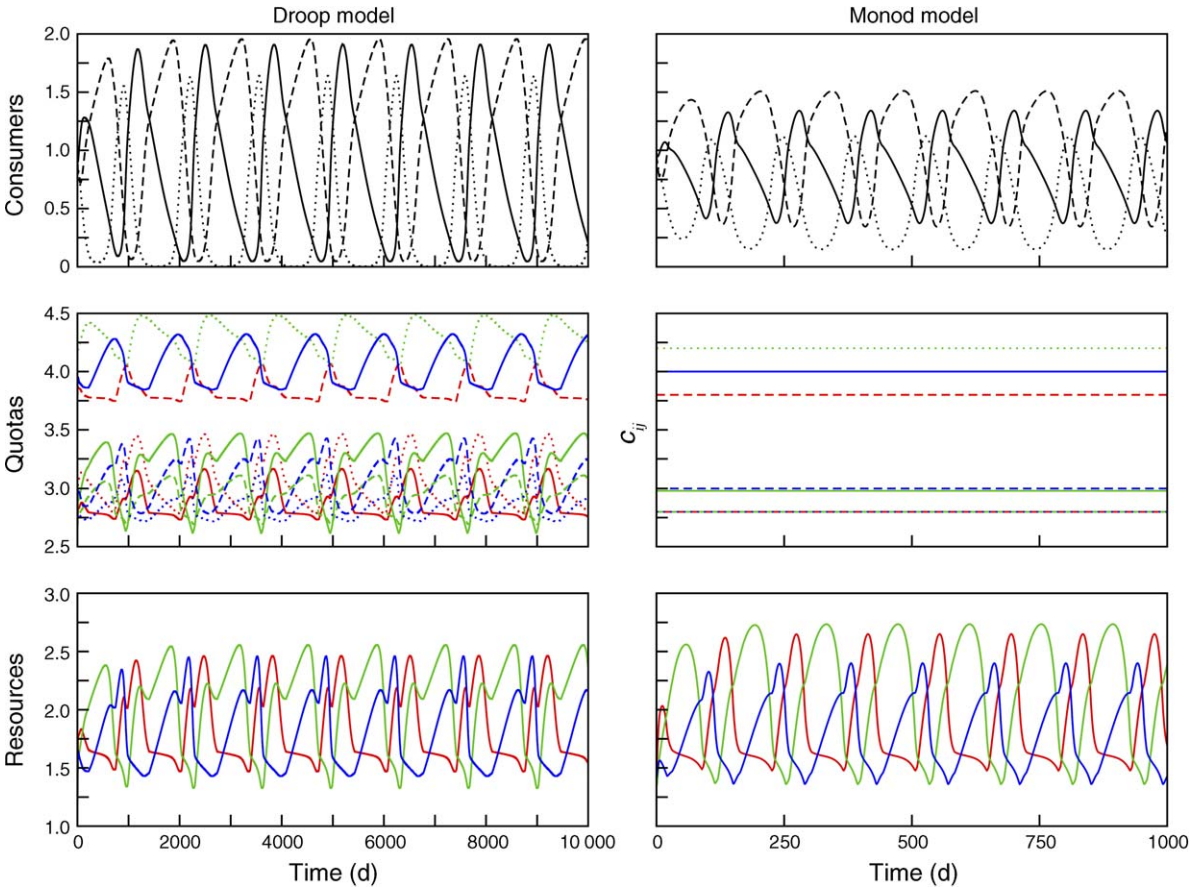

FIG. 3. Dynamics of consumers, quotas, and resources for a Droop model and an equivalent Monod model, i.e., a model with the same resource requirements, quotas, and uptake rates as the Droop model has at equilibrium. Resources are indicated by colors (1, red; 2, green; 3, blue), and consumers by line patterns (1, solid; 2, dashed; 3, dotted). For the Monod model, the fixed resource contents c_{ji} are shown for comparison with the quotas Q_{ji}.

all 100 000 simulations for scenario 1. When all species consumes least of the resource for which they have highest requirements, one of the three species outcompetes the other two (Fig. 2B). In all simulations based on scenario 3, we similarly obtained competitive exclusion, with the winner depending on the initial conditions.

Nonequilibrium outcomes were obtained for scenario 2, where each species consumes most of the resource for which it has intermediate requirements. We obtained regular limit cycles with a constant period as in Fig. 2C or oscillations with increasing period as in Fig. 2D. The latter type corresponds to a heteroclinic orbit connecting the three monoculture equilibria.

Fig. 3 illustrates that the competition induced oscillations are somewhat different than those of the Monod model. In this figure, the dynamics of a Droop model (left panels) are compared with those of the "corresponding" Monod model, i.e., a Monod model with the same community equilibrium, the same external resource requirements R_{ji}^*, and the same consumption patterns $c_i = 1/m_i[\mathbf{f}_i(\hat{\mathbf{R}})] = 1/D[\mathbf{f}_i(\hat{\mathbf{R}})]$. In line with many similar simulations, the Monod model displays a much higher oscillation frequency (notice the time scale). Apart from this, the oscillations of external resource concentrations and species densities look rather similar in both models, despite oscillations of the resource contents in the Droop model (in the Monod model, the resource contents are constant by definition). However, in the Droop model the pattern of oscillations tends to be somewhat more complex at the resource level and somewhat less complex at the level of species densities. Interestingly, the oscillations of consumer densities are more pronounced than in the Monod model, despite of the (presumably) buffering effect of nutrient storage.

To investigate whether the outcomes in Figs. 2C, D and 3 are representative, we again ran many simulations. In 20–25% of cases (depending on the search window in parameter space), we obtained regular oscillations as in Fig. 2C, where all species stayed well above zero in density. In about 60% of cases, we obtained either oscillations involving very low species densities ($<10^{-4}$) or heteroclinic cycles as in Fig. 2D. In a heteroclinic cycle, the system stays close to a monoculture equilibrium for increasingly long periods of time, once in a

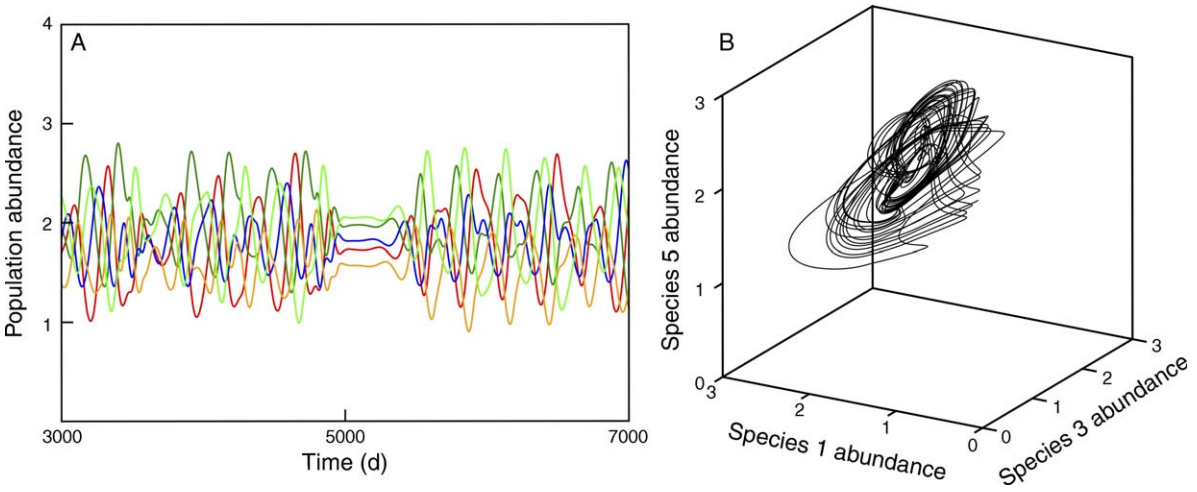

FIG. 4. Competitive chaos for five species competing for five resources. (A) Time series illustrating how an apparently stable period is followed by violent fluctuations. (B) The chaotic attractor for the same series plotted for species 1, 3, and 5 for $t = 10\,000$–$20\,000$.

while rapidly switching from one monoculture to another. Hence, for long periods of time, two of the three species have very low densities. Accordingly, in a real-world system such a situation would lead to the extinction of two of the three species, corresponding to competitive exclusion. In contrast with the Monod model, we also obtained "theoretical competitive exclusion" in 15–20% of our simulations. In these cases, the system converged to an asymptotically stable monoculture equilibrium. To understand this, notice that the scenarios in Table 1 are only valid at the community equilibrium. In contrast to the Monod model, the hierarchy of consumption patterns may change in time, leading, for example, to a switch from the "rock–scissors–paper" scenario 2 to a scenario favoring competitive exclusion. In conclusion, nutrient storage and luxury consumption change the rules of the game, making oscillations (slightly) less likely than in the Monod model.

Competition for more than three resources

With the same reservations as in the case $n = k = 3$, the results of Huisman and Weissing (2001) seem to extend to more than three resources. With four species and four resources (results not shown) our simulations revealed stable equilibrium coexistence if at equilibrium each species consumes most of the resource for which it has the highest requirement; and competitive exclusion if each species consumes most of the resource for which it has the lowest requirement. We also found oscillations with either constant or increasing period when consumption is higher on resources for which the requirements are intermediate. In some cases, as in Huisman and Weissing (2001), if each species consumes most of the resource for which it has the second-highest requirement, one species pair displaces the other species pair; the winning pair depending on the initial conditions.

With five species competing for five resources, competitive oscillations with switching partners occur if each species consumes most of the resource for which it has the second-highest requirement. But if each species consumes most of the resource for which it has the intermediate requirement, the system can generate chaos. In Fig. 4, we show one of these chaotic time series, which displays an apparent period of stabilization followed by violent fluctuations again. For a given set of physiological and environmental parameters the system may have alternative attractors. This is exemplified by Fig. 5, where the system may, depending on the initial conditions, end up in a limit cycle, a heteroclinic cycle or a non-periodic attractor.

More species than resources: supersaturation

In light of the previous results, the question arises whether, as in the Monod model, internally generated nonequilibrium conditions allow supersaturation, i.e., the coexistence of more species than the number of resources (Huisman and Weissing 1999). The answer is yes. Fig. 6 shows oscillatory coexistence of four, five, and six species on three resources. These oscillations can have low or high amplitudes. Fig. 6A is particularly interesting; here the invasion of a fourth species actually leads to a reduction in the amplitude of oscillations, making the system look more "equilibrium-like."

DISCUSSION

Storage-based models proved able to display as rich dynamics as their constant resource content counterparts (e.g., the Monod model). This is a new confirmation that multispecies competition can display sustained oscillations, with no need of externally imposed fluctuations. The mechanism is the same in both models: nontransitivity in competitive dominance (Huisman and Weissing 2001). If species dominance relationships are

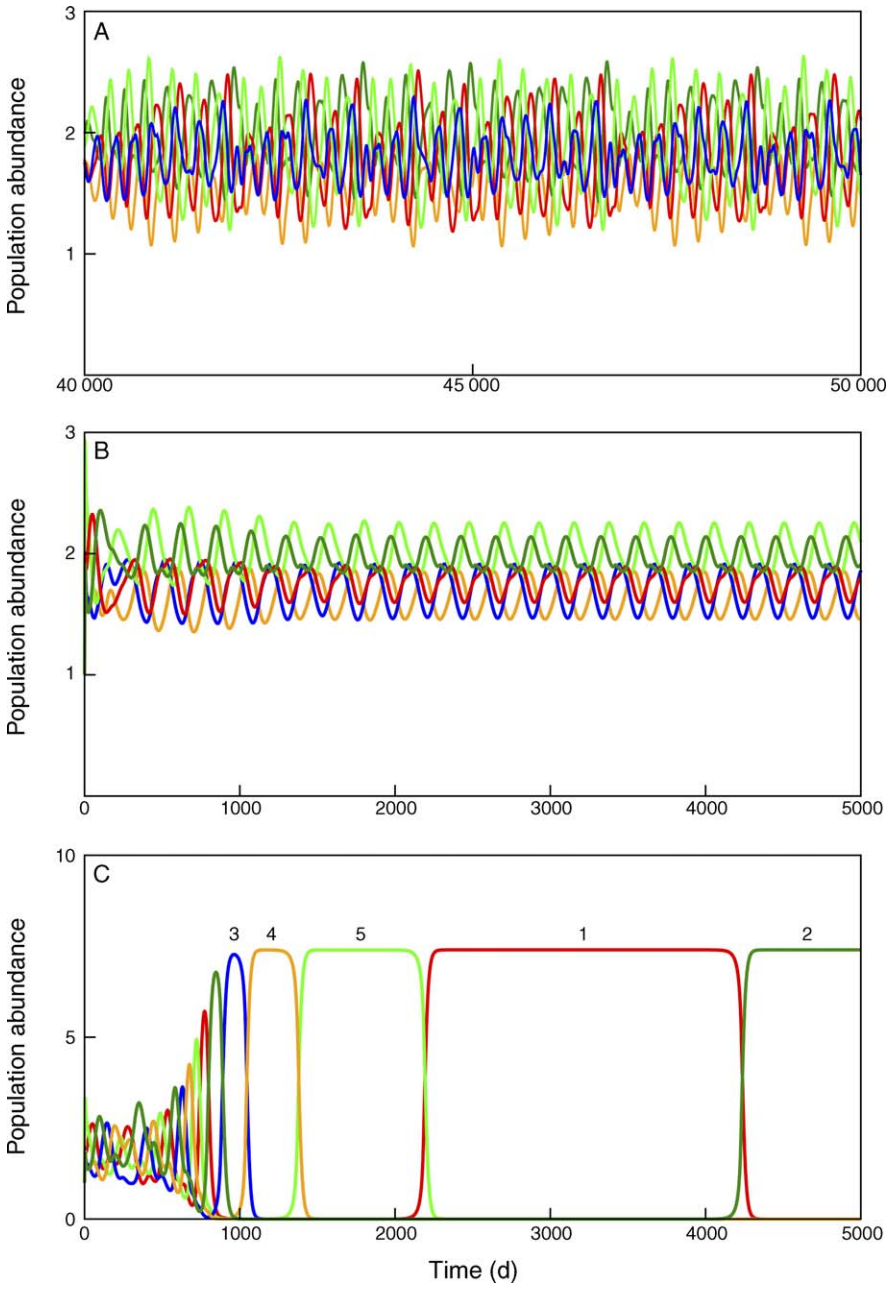

FIG. 5. Coexisting attractors in the case of five species competing for five resources. For a given set of parameters, each graph corresponds to a different initial condition for the fifth species: (A) $N_5(0) = 0.9$, non-periodic oscillations; (B) $N_5\ (0) = 1.5$, limit cycle; (C) $N_5(0) = 1.8$, heteroclinic cycle.

not transitive (A beats B, B beats C, but C beats A), the community equilibrium is unstable, so that oscillations or chaos occur. Moreover, many, if not all, of the boundary equilibria of the community are unstable, preventing species from going extinct and promoting high diversity and supersaturation (Fig. 6). It is worth noticing that a variety of modeling approaches (Gilpin 1975, May and Leonard 1975, Huisman and Weissing 1999, Laird and Schamp 2006) point toward the general conclusion that non-transitivity in competitive hierarchy promotes coexistence, or alternatively, delays competitive exclusion, enhancing biodiversity.

Mathematical analysis of the Monod model (Huisman and Weissing 2001, Li 2001) revealed that the stability of the community equilibrium is crucially dependent on the consumption pattern, i.e., the matrix of consumption terms c_{ji}. In a separate paper (T. Revilla and F. J. Weissing, *unpublished manuscript*), we show analytically that the same is true for storage models in general. In line with a recent study of Li and Smith (2007), who

perform a global analysis for the special case $n = k = 2$, we arrive at the conclusion that the dynamic behaviour of both types of model is qualitatively very similar close to equilibrium.

Still, there are important differences between both types of model. Most importantly, the consumption terms in the Droop model are no longer fixed but functions $f_{ji}(R_j)$ of the external resource concentrations. Accordingly, it is not possible to separate resource requirements and consumption patterns, as in the Monod model. In the Monod model, the positive cone in resource space allowing stable coexistence (like the wedge in Fig. 1B), looks the same irrespective of the position of the resource equilibrium $\hat{\mathbf{R}}$. In the Droop model, luxury consumption of non-limiting resources has the effect that the corresponding cone (spanned by the consumption vectors $f_{ji}(R)$) gets smaller and smaller when the resource equilibrium $\hat{\mathbf{R}}$ is approached from the direction of the resource supply point. Accordingly, luxury consumption results in a decrease of the zone of stable coexistence. Thus, the multispecies quota models seem to be more likely to end up displaying unstable community equilibria. When the community equilibrium is unstable the resulting dynamics could be nonequilibrium coexistence or competitive exclusion.

According to our simulations, the Droop model has a lower tendency for oscillations than the Monod model, because the consumption pattern at equilibrium may change as the system evolves, as well as the identity of the resource that causes growth limitation for a given species. Theoretically, such changes might allow oscillations in cases where such oscillations cannot occur in the Monod model. We never encountered a simulation corresponding to this possibility, perhaps because we focused on the cases $k = 3$, 4, and 5. There is however, another potential mechanism that may cause oscillations in models with nutrient storage. In fact, damped oscillations occur in the single-species Droop model if the mortality rate m is large enough when compared to the flow rate D (Clodong and Blasius 2004), this will never happen if $m = D$ (Lange and Oyarzun 1992, Oyarzun and Lange 1994, Legovic and Cruzado 1997). It was for this reason that we made the chemostat assumption, since we were mainly interested in competition-induced oscillations. Since we ran only few simulations with $m_i > D$, it is an open problem whether or not such fluctuations of physiological origin could interact synergistically with competitive-induced oscillations, enhancing the chances of nonequilibrium coexistence.

Toward a realistic theory of trade-offs

We have seen that the occurrence of nonequilibrium dynamics strongly depends on trade-offs between resource requirements and consumption rates. In the context of the Monod model, it is difficult to develop a mechanistic theory of such trade-offs, since already the underlying growth equation (Eq. 2; corresponding to a numerical response) lacks a mechanistic underpinning. In contrast, the uptake function (Eq. 5; corresponding to a functional response of Holling [Holling 1959] type II) of the Droop model can be justified mechanistically in terms of physiological and environmental factors (e.g., transporter properties, cell size, medium viscosity, temperature).

For example, Aksnes and Egge (1991) have shown that the maximum uptake rate v_{ji} for a given nutrient is directly proportional to the number n_{ji} of nutrient-specific transporters. If each transporter occupies an area a_{ji} on the surface of the cell membrane, a natural constraint arises, since $\Sigma\, a_{ji}n_{ji} \leq A_i$, where A_i denotes the total surface available. If we further assume that surface area scales with cell mass w_i with a certain allometric exponent ρ (i.e., $A_i \propto w_i^{\rho}$), we get an allometric constraint for the maximum uptake rates of the form $\Sigma\, a_{ji}v_{ji} \leq kw_i^{\rho}$. Thus, raising the maximum uptake v_{ji} for resource j may be associated by a decrease in the maximum uptake of other resources, unless the cell size is increased too. An increase in cell size would in turn have other metabolic costs, reflected as increased threshold requirements q_{ji}.

To illustrate the use of a mechanistic interpretation of trade-offs, consider the following argument. For the second scenario in Table 1, we obtained competitive exclusion in a considerable number of cases where an equivalent Monod model would predict oscillations. When we looked at these cases in detail, it turned out that the v_{ji} and K_{ji} yielded uptake functions that cross each other, like in Fig. 7. This means that the consumption hierarchies can change as the system evolves, leading, for example, to a hierarchy inducing competitive exclusion. A situation as in Fig. 7 can easily arise if the parameters v_{ji} and K_{ji} happen to be positively related. This is precisely what the model of Aksnes and Egge predicts, since both v_{ji} and K_{ji} are proportional to the handling time needed to pass a nutrient molecule through the membrane. In our simulations, we unintendedly also introduced a positive correlation among v_{ji} and K_{ji} (see Appendix A). Accordingly, we encountered a relatively large number of situations were the rules of the competitive game at equilibrium change drastically when moving away from equilibrium. If v_{ji} and K_{ji} were negatively correlated instead, the consumption hierarchies of Table 1 are more likely to remain stable, as in the Monod model.

Stoichiometry

For both the Monod and the Droop model, oscillations can only occur if species differ in their resource requirements and in their resource uptake characteristics in a specific and contrasting way (e.g., scenario 2 in Table 1). In nature, variation in resource contents and requirements occur within the limits allowed by the stoichiometry of the underlying biochemical reactions. One may therefore wonder whether our theoretical

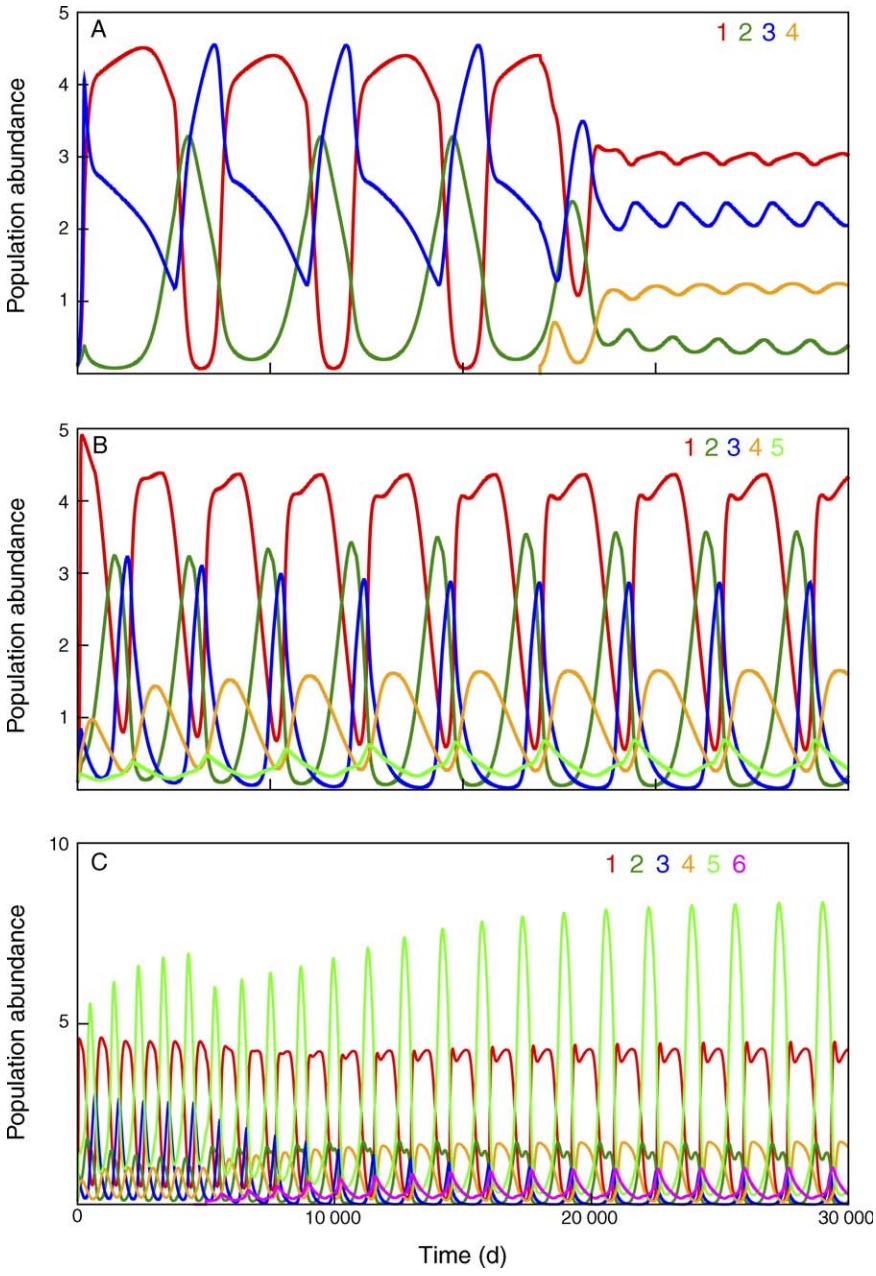

FIG. 6. Nonequilibrium coexistence of 4, 5, and 6 species on three limiting resources. (A) High-amplitude oscillations of three species allows the invasion of a fourth species (introduced at $t = 6000$ d). The system ends up displaying low-amplitude oscillations. (B) Oscillations of five species competing for three resources. (C) Oscillations of six species competing for three resources (species 6 invades at $t = 5000$ d).

considerations are compatible with such stoichiometric constraints.

First, one might think that species cannot differ too much in their hierarchy of resource requirements R_{ji}^* or in their hierarchy of quotas at equilibrium $\hat{Q}_{ji}$. It is, for example, well known that organisms cannot have a lower content (grams or moles) of carbon (C) than their contents of nitrogen (N) or phosphorous (P), no matter how flexible the variable quotas are. For algae, the canonical stoichiometric reference are the Redfield (1958) ratios for atomic composition, C:N:P = 106:16:1. However, recent work (Legovic and Cruzado 1997, Klausmeier et al. 2004*a*, *b*) indicates that Redfield ratios are not cast in stone but actually quite variable. Due to this flexibility, it is not unrealistic that each resource has a different hierarchy across species with respect to either resource contents or resource requirements. This is illustrated by Table 2, showing three species resource

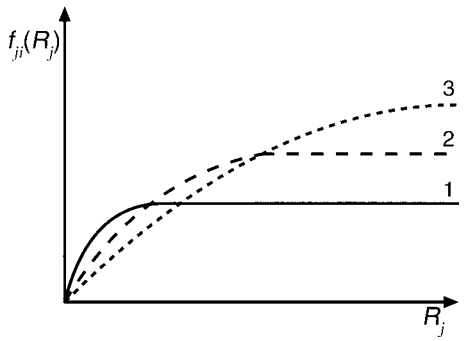

FIG. 7. Change in uptake hierarchies due to mechanistic constraints. If the maximum uptake rate v_{ji} and the half-saturation constant K_{ji} are positively correlated, as predicted by mechanistic theory, the resource uptake functions of three species can easily cross. As a consequence, the ranking of the species with respect to resource uptake (as in Table 1) changes with the resource concentration.

contents coming close to Redfield ratios. In this example, species 1 has the highest content of P, species 2 of C, and species 3 of N. Similarly, we can build any hierarchy for resource requirements. We can conclude that stoichiometric principles like the Redfield ratios only impose mild constraints on the hierarchies of requirements and quotas.

Second, one might think that, even if hierarchies differ between species, for each given species, the hierarchy of resource requirements should roughly match the hierarchy of resource consumption. In fact, one might argue that scenario 1 in Table 1 is much more likely than the other two scenarios: according to Eq. 7, external (R_{ji}^*) and internal (Q_{ji}^*) requirements are positively related, implying, that the hierarchy of R^*- and Q^*-values are not to be different. Because of $\hat{f}_{ji} = m_i \hat{Q}_{ji}$, the hierarchy of uptake patterns $\hat{f}_{ji}$ should roughly match the hierarchy of equilibrium quotas $\hat{Q}_{ji}$, at least if the m_i are not too different (as in a chemostat, where $m_i = D$). Does this not imply that the hierarchies of R^*-values should correspond to the hierarchy of $\hat{f}$-values, as in scenario 1 of Table 1? The answer is no. First, luxury consumption causes a mismatch between Q_{ji}^* and $\hat{Q}_{ji}$, implying that the relationship between R_{ji}^* and $\hat{Q}_{ji}$ is far from obvious. Second, already the relationship between R_{ji}^* and Q_{ji}^* is not really obvious, since the parameters v_{ji} and K_{ji} in Eq. 7 are both species and resource specific. According to theories like those of Aksnes and Egge (1991), these parameters depend on many details that are not related with the rules of internal metabolism or the stoichiometry underlying biochemical reactions. Accordingly, we do not see a reason for stoichiometry to prevent specific patterns of resource requirements and resource consumption.

CONCLUSION

Our simulations show that multispecies resource competition models with storage dynamics like the Droop model can display the competitive oscillations that are common in other models (Gilpin 1975, May and Leonard 1975, Huisman and Weissing 1999). In addition they can also generate coexistence of more species than the number of resources. The mechanism behind the oscillations is the sequence of replacements of species due to the lack of absolute winners in the total ensemble of species as in the "rock–scissors–paper" game, a condition that results from trade-offs between resource requirements and consumption patterns. The implicit delay by which a species responds to resource fluctuations in the external medium does neither cause nor enhance these oscillations. In fact, it retards the oscillations considerably, leading to periods that are one or more orders of magnitude longer than those in corresponding models without storage. Moreover, in a considerable percentage of cases oscillations do not occur in models with storage, while they are to be expected on basis of the corresponding models without storage. This discrepancy is caused by luxury consumption that may destroy the intransitivity causing oscillations (as in the rock–scissors–paper game) as soon as the system is sufficiently far from equilibrium. Storage models are considerably more complex than purely phenomenological models like the Lotka-Volterra models or less detailed semi-mechanistic models like the Monod model. But physiological models accounting for storage have the big advantage that the all-important trade-offs can be given a much better interpretation.

TABLE 2. Hypothetical example of three species that, despite similar C:N:P ratios, differ in the hierarchy of their resource contents.

Resource	Species 1	Species 2	Species 3
C	1045	1060	1053
N	165	160	171
P	11	10	9
C:N:P	95:15:1	106:16:1	114:19:1

ACKNOWLEDGMENTS

We thank Jim Grover and an anonymous reviewer for their helpful comments on a previous version of the manuscript. T. Revilla was supported by a grant from the Netherlands Organization for Scientific Research (NWO).

LITERATURE CITED

Aksnes, D. L., and J. K. Egge. 1991. A theoretical model for nutrient uptake in phytoplankton. Marine Ecology Progress Series 70:65–72.

Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist 115:151–170.

Burmaster, D. E. 1979. The continuous culture of phytoplankton: mathematical equivalence among three steady-state models. American Naturalist 113:123–134.

Clodong, S., and B. Blasius. 2004. Chaos in a periodically forced chemostat with algal mortality. Proceedings of the Royal Society of London B 271:1617–1624.

Droop, M. R. 1973. Some thoughts on nutrient limitation in algae. Journal of Phycology 9:264–272.

Ducobu, H., J. Huisman, R. R. Jonker, and L. R. Mur. 1998. Competition between a prochlorophyte and a cyanobacteri-

um under various phosphorous regimes: comparison with the Droop model. Journal of Phycology 34:467–476.
Gilpin, M. E. 1975. Limit cycles and competition in communities. American Naturalist 109:51–60.
Grover, J. P. 1997. Resource competition. Chapman and Hall, London, UK.
Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.
Huisman, J., A. M. Johansson, E. O. Folmer, and F. J. Weissing. 2001. Towards a solution of the plankton paradox: the importance of physiology and life history. Ecology Letters 4:408–411.
Huisman, J., and F. J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402:407–410.
Huisman, J., and F. J. Weissing. 2001. Biological conditions for oscillations and chaos generated by multispecies competition. Ecology 82:2682–2695.
Huisman, J., and F. J. Weissing. 2002. Oscillations and chaos generated by competition for interactively essential resources. Ecological Research 17:175–181.
Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist 95:137–145.
Klausmeier, C. A., E. Litchman, T. Daufresne, and S. A. Levin. 2004*a*. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. Nature 249:171–174.
Klausmeier, C. A., E. Litchman, and S. A. Levin. 2004*b*. Phytoplankton growth and stoichiometry under multiple nutrient limitation. Limnology and Oceanography 49:1463–1470.
Kooijman, S. A. L. M. 2000. Dynamic energy and mass budgets in biological systems. Second edition. Cambridge University Press, Cambridge, UK.
Laird, R. A., and B. S. Schamp. 2006. Competitive intransitivity promotes species coexistence. American Naturalist 168: 182–193.
Lange, K., and F. J. Oyarzun. 1992. The attractiveness of the Droop equations. Mathematical Biosciences 111:261–278.
Legovic, T., and A. Cruzado. 1997. A model of phytoplankton growth on multiple nutrients based on the Michaelis-Menten-Monod uptake, Droop's growth and Liebig's law. Ecological Modelling 99:19–31.
León, J. A., and D. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. Journal of Theoretical Biology 50:185–201.
Li, B. 2001. Periodic coexistence in the chemostat with three species competing for three essential resources. Mathematical Biosciences 174:27–40.
Li, B., and H. L. Smith. 2003. Periodic coexistence of four species competing for three essential resources. Mathematical Biosciences 184:115–135.
Li, B. T., and H. L. Smith. 2007. Global dynamics of microbial competition for two resources with internal storage. Journal of Mathematical Biology 55:481–515.
May, R. M., and W. J. Leonard. 1975. Nonlinear aspects of competition between three species. SIAM Journal of Applied Mathematics 29:243–453.
Monod, J. 1950. La technique de culture continue, theorie et applications. Annales d'Institute Pasteur 79:390–410.
Oyarzun, F. J., and K. Lange. 1994. The attractiveness of the Droop equations II. Generic uptake and growth functions. Mathematical Biosciences 121:127–139.
Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist 46:205–221.
Schippers, P., A. M. Verschoor, M. Vos, and W. M. Mooij. 2001. Does "supersaturated coexistence" resolve the "paradox of the plankton"? Ecology Letters 4:404–407.
Smith, H. L., and P. Waltman. 1994. Competition for a single limiting resource in continuous culture: the variable-yield model. SIAM Journal of Applied Mathematics 54:1113–1131.
Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58: 338–348.
Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
Turpin, D. H. 1988. Physiological mechanisms in phytoplankton resource competition. Pages 316–368 *in* C. Sandgren, editor. Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge, UK.
Von Liebig, J. 1840. Die Organische Chemie in ihrer Anwendung auf Agrikultur und Physiologie. Friedrich Vieweg, Braunschweig, Germany.

APPENDIX A

Simulation details (*Ecological Archives* E089-050-A1).

APPENDIX B

Parameter values (*Ecological Archives* E089-050-A2).

SUPPLEMENT

Source code for simulations (*Ecological Archives* E089-050-S1).